and conspicuous at this station on the outer coastal plain. We have never encountered it elsewhere in eastern North Carolina. Interestingly, it has not been found in adjacent southeastern Virginia.—DIVISION OF BIOLOGICAL SCIENCES: BOTANY, NORTH CAROLINA STATE COLLEGE, RALEIGH, NORTH CAROLINA AND DEPARTMENT OF BOTANY, DUKE UNIVERSITY, DURHAM, NORTH CAROLINA.

SOME CRUCIFERAE OF THE NASHVILLE BASIN, TENNESSEE

REED C. ROLLINS

THE affinity of many representatives of the Cruciferae for limestone and gypseous areas is well known. Evidently the highly calcareous soils of the Nashville Basin (Fenneman, 1938) have provided particularly suitable habitats for the extensive development of two genera of the Cruciferae. All four species of the unique genus *Leavenworthia* are found in this relatively small area and two of them are largely confined to it (Baldwin, 1945). Plants of *L. aurea*, *L. stylosa*, *L. torulosa*, and *L. uniflora* are extremely abundant in the open glades, pastures and old fields at particular locations, often covering several to many acres of land. The opportunity for hybridization between the species of *Leavenworthia* is certainly present, for they occur together in some places. In my own experience, *L. stylosa* and *L. uniflora* were found together at two locations, but mostly the species were in pure stands. In some instances these were not separated by more than a few hundred yards. Gattinger in a letter to Gray (cf. Baldwin, l. c.) claims to have found three species in one square yard of ground near Nashville. Certainly the types of habitats in which all species occur in the Nashville Basin are very similar. I noticed a tendency for *L. uniflora* to invade old cornfields where the plants often covered a field of a dozen acres or more. This species tends to flower earlier than the other three and is the most distinctive, but all species can be found flowering at the same time and growing in close proximity, if not together, in a number of locations. Many plants in several such localities were carefully examined for traces of introgressive hybridization. However, no evidence that natural hybridization occurs between any combination of the species could be found. It seems safe to conclude that hybridization is not a major factor in producing the variability that does occur in the species in central Tennessee.

Though the Nashville Basin is certainly today the center of variability and the area of perhaps the highest concentration of numbers of individuals of *Leavenworthia*, it cannot be assumed that the genus originated there nor that the primary speciation took place within its bounds. The possibility of a southwestern origin (e. g. in the Texas area), in view of the facts with regard to *Lesquerella*, should receive attention.

Lesquerella

There is a striking parallel between *Leavenworthia* and *Lesquerella* with respect to their distribution in Tennessee. Four species of each genus are to be found in the Nashville Basin. Members of the two genera are usually not found growing together but each species tends to be abundant where it is found. The species of both genera have weedy tendencies, quickly invading fields and pastures. The one exception is *Lesquerella globosa*. To one accustomed to whole fields of Cruciferae only when members of old world weeds such as *Brassica*, *Sisymbrium*, *Thlaspi*, *Isatis* or *Cardaria* were rampant, it was indeed strange to see *Lesquerella* and *Leavenworthia* playing the same role in middle Tennessee. Even more disturbing was the realization, while viewing these fields, that two of the species of *Lesquerella* were undescribed and unknown to botanists generally.

Lesquerella, with numerous representatives in the intermountain area of western North America, has its largest concentration of species in Texas and northeastern Mexico. With this in mind, Payson (1922) found it difficult to understand the isolation and very limited range of *L. Lescurii* then known only from the vicinity of Nashville. Now a slightly enlarged area of distribution for this species is known, as the data below show, but even this is a decidedly restricted area for a species that is exceedingly abundant when it is found and shows weedy tendencies by invading sites disturbed by man. *L. globosa*, a wholly unrelated species, is found not far from Nashville and its range extends into Kentucky, with a single known station in southeastern Ohio.[1] The isolation of these two species from the main body of the genus, their lack of relatedness to each other, and the fact that they occurred more or less in the same area was a hard combination to explain. Payson was puzzled as to the relationships of *L. globosa* and our knowledge of this species is not sig-

[1] The single Ohio collection reported by Jones (1940) has not been seen.

nificantly improved from that known by him. Its true relationships may ultimately become evident from further studies of other species of the genus. Of one thing we can be sure, *L. globosa* is not a close relative of the other species of *Lesquerella* found in the same area.

We now know that *L. Lescurii* is but one of three related species, all localized and well within the boundaries of the Nashville Basin. Some help in understanding the problem of isolation from the main body of the genus may be drawn from a consideration of these newly discovered species of *Lesquerella*. The new species, *L. densipila* and *L. perforata* are related to each other and to *L. auriculata* and *L. grandiflora*, species of Texas and Oklahoma. They also have some characteristics in common with *L. Lescurii*, a fact that strengthens the position of this somewhat anomalous species as a true member of *Lesquerella*. *L. Lescurii* now appears to tie in with the main body of the genus through *L. densipila* and *L. perforata*.

One of the two new plants, *L. perforata*, is of considerable morphological interest. The interior surfaces of the valves are densely covered with small dendritic trichomes. The presence of trichomes on the interior of the silique is not known in any other species of *Lesquerella*, and this is a fairly rare phenomenon in the Cruciferae. In certain species of *Cibotarium* such as *C. divaricatum*, *C. macropetalum* and *C. macrum*, trichomes are found on the inner surfaces of the valves. Similarly, they occur in *Farsetia triquetra*, but I have not seen them in any other member of the Cruciferae. A second peculiarity in *L. perforata* is the absence of a complete septum. In some siliques, the septum appears to be lacking entirely, while in others there is only a narrow band of septum tissue attached to the inner margin of the replum. In the majority of *Lesquerella* species, the septum is entire. Exceptions are found in such species as *L. arctica*, *L. condensata*, *L. utahensis* and *L. occidentalis* but the perforations in all instances where I have observed them are not nearly so large as in *L. perforata*. The significance of the presence of an indument on the inner surface of the siliques of *L. perforata* is not at present assessable in terms of the genus as a whole. Certainly this is worthy of further study as a problem apart from a taxonomic treatment of the genus.

All three species of *Lesquerella* that are confined to the Nashville Basin, i. e. *L. densipila*, *L. Lescurii* and *L. perforata*, show

considerable variation. There is some indication that variants are becoming established as populations, as indicated by the fact that *L. densipila*, var. *maxima* is separable, and it may be supposed that new variations are constantly arising. It is my distinct impression from initial field studies that these species are favorably situated for relatively rapid evolutionary differentiation. The solution to the phytogeographic problem posed by *Leavenworthia* and these isolated species of *Lesquerella* needs considerably more field study. However, I find it tempting to offer as an explanation the assumption that representatives of both genera migrated from the southwest into the Nashville Basin area. Once in such a favorable locality for evolutionary differentiation, each has produced a number of distinct species. The fact that interspecific hybridization does not appear to be a factor in producing present-day variation in *Leavenworthia* suggests that genetic barriers have paralleled the morphological distinctions that have evolved in that genus. I am less confident that interspecific hybridization has not played a part in producing some of the variant populations of *Lesquerella* in the Nashville Basin. On the other hand, I do not have any positive evidence that the different species hybridize naturally.

Following is a synoptic treatment of *Lesquerella* for the State of Tennessee:

KEY TO THE SPECIES

Siliques strongly flattened parallel to septum, valves hirsute with bulbous-based trichomes.....1. *L. Lescurii.*

Siliques globose to pyriform, inflated, not flattened, valves finely pubescent to sparingly hirsute with nonbulbous-based trichomes.

Cauline leaves auriculate, clasping the stem; stems and leaves with spreading simple or branched trichomes; style shorter than the silique.

Siliques glabrous within, globose to subglobose, densely pubescent with short erect trichomes on the exterior; septum present; petals yellow or white, obovate.

Trichomes of siliques minute, visible only with magnification; petals yellowish orange.....2a. *L. densipila*, var. *densipila.*

Trichomes of siliques comparatively large and prominent, visible without magnification; petals white with a yellow claw, occasionally yellowish.....2b. *L. densipila*, var. *maxima.*

Siliques densely pubescent within, pyriform to depressed-pyriform, glabrous to sparsely pubescent with large trichomes on the exterior; septum absent; petals white, spatulate.....3. *L. perforata.*

Cauline leaves narrowed at base, nonauriculate, not clasping the stem; stems and leaves covered with appressed stellate trichomes; style about twice the length of the silique.....4. *L. globosa.*

1. **Lesquerella Lescurii** (Gray) S. Wats. Proc. Amer. Acad. 23: 250. 1888.

Vesicaria ? Lescurii Gray, Manual, ed. 2, 38. 1856.
Alyssum Lescurii Gray, Manual, ed. 5, 72. 1867.

Known only from Tennessee and restricted to the central counties as follows: Cheatham Co.—roadside, state highway No. 12, 11 miles northwest of Bordeaux, March 31, 1952, *Reed C. and Diane Rollins 5212* (G[2]); Davidson Co.—dry hills near Nashville, April, *L. Lesquereux* (G, type); Nashville, 1878, *Dr. A. Gattinger* (G); same locality, May, 1906, *Albert Ruth 360* (G); same locality, 1896, *S. O. Barnes s. n.* (G); same locality, March 30, 1952, *Reed C. and Diane Rollins 5209* (G); same locality, April 1914, *W. H. Manning s. n.* (G); same locality, April, 1936, *H. K. Svenson 7525* (G); Peabody Campus, Nashville, April, 1940, *Jesse M. Shaver 6574* (G, P); thin soil in abandoned field, Nashville, April 20, 1940, *A. J. Sharp and R. E. Shanks 454, Plantae Exsiccatae Grayanae no. 1053* (G, UT); same locality, May, 1941, *A. J. Sharp 1529* (UT); Williamson Co.—two miles north of Nolensville, March 31, 1952, *Reed C. and Diane Rollins 5214* (G); Rutherford Co.—open field near Smyrna, March 30, 1934, *Harold Bold and A. J. Sharp 41* (UT); open field, nine miles northwest of Murfreesboro, April 1, 1952, *Reed C. and Diane Rollins 5224* (G), Wilson Co.—between Nashville and Lebanon, April 1, 1934, *A. J. Sharp 78* (UT).

2. **Lesquerella densipila** Rollins, sp. nov.

Annual; stems several to numerous, erect or the outer decumbent at base, simple or branched, purplish below, 1–4 dm. high, hirsute below with spreading simple trichomes, rachis of inflorescence and upper portion of stems hirsute with smaller less-spreading and frequently branched trichomes; basal leaves petiolate, lyrately pinnatifid to pinnately lobed, obtuse, 4–8 cm. long, 1–1.8 cm. wide, terminal lobe comparatively large, lateral lobes decurrent on rachis, hirsute on upper surface with mostly simple trichomes, lower surface with a mixture of large simple and smaller branched trichomes; cauline leaves sessile, auriculate, broadly ovate to oblong, 1–3 cm. long, 0.5–1.5 cm. broad, lower broadly obtuse, upper smaller and tending toward acuteness, dentate to nearly lobed, hirsute on both surfaces with mostly simple spreading trichomes; inflorescence racemose, 1–2 dm. long; fruiting pedicels divaricately ascending, straight, expanded at summit, 1–2 cm. long, pubescent with a mixture of simple and branched trichomes; sepals non-saccate, sparsely to generally covered with appressed branched trichomes, oblong, alternating members flat and boat-shaped, narrowed toward apex but remaining rounded, 2.5–4.5 mm. long, 1.5–2 mm. wide; petals yellow to white, broadly obovate, not markedly differentiated into blade and claw, 6–8 mm. long, 4–5 mm. wide; filaments strongly dilated at base, attached to anthers just below middle,

[2] Citations of specimens are as follows: Gray Herbarium (G); Herbarium of Jesse M. Shaver, Peabody College, Nashville (P); Herbarium of Vanderbilt University, Nashville (V); Herbarium of the University of Tennessee (UT).

anthers nearly versatile, ca. 1.5 mm. long; glandular tissue in a thin continuous mold beneath stamens, forming projections between single and paired stamens and an abbreviated ring around the base of the filament of the single stamens; siliques subglobose to slightly broader than long, uncompressed, 3–4.5 mm. in diameter, densely pubescent with minute to longer simple or branched spreading trichomes; styles 2–3 mm. long, pubescent below, glabrous above, slightly expanded into a capitate stigma; ovules 4–5 in each loculus, funiculi free except at their very base; replum nearly orbicular; seeds immature, flattened, orbicular.

Herba annua; caulibus erectis hirsutis 2–4 dm. altis; foliis radicalibus lyratis vel runcinatis hirsutis 4–8 cm. longis, 1–1.8 cm. latis; foliis caulinis sessilibus auriculatis dentatis hirsutis 1–3 cm. longis, 0.5–1.5 cm. latis; pedicellis divaricatis 1–2 cm. longis; sepalis oblongis pubescentibus; petalis obovatis flavis vel albis 6–8 mm. longis; siliquis subglobosis sessilibus 3–4.5 mm. diametro pubescentibus; stylis 2–3 mm. longis; loculis 4–5 ovulatis; seminibus immaturis orbiculatis immarginatis.

2a. **L. densipila,** var. **densipila**

Flowers yellowish orange; siliques densely covered with minute simple or branched trichomes (Fig. 1). Type in the Gray Herbarium collected in the Duck River bottom, north of Verona, Marshall County, Tennessee, April 10, 1949, *A. J. Sharp, C. J. Felix and Wm. Adams 11187*. Other collections:—near Duck River, three miles south of Chapel Hill, Marshall County, March 31, 1952, *Reed C. and Diane Rollins 5217* (G); abundant annual in open glade, one mile north of College Grove, Williamson County, March 31, 1952, *Reed C. and Diane Rollins 5215* (G).

2b. **L. densipila,** var. **maxima** Rollins, var. nov.

Flowers white or occasionally yellowish; siliques densely covered with much longer trichomes than in var. *densipila*.

Herba annua; petalis albis vel luteis; siliquis dense pilosis.

Type in the Gray Herbarium, collected in an open field, 12 miles southeast of Nashville on the Lavergne-Couchville Pike, Davidson County, Tenn., April 1, 1952, *Reed C. Rollins, Diane Rollins, and Elsie Quarterman 5223*. Also collected near roadside, 10 miles southeast of Nashville, Lavergne-Couchville Pike, April 1, 1952, *Reed C. Rollins, Diane Rollins, and Elsie Quarterman 5222* (G); roadside in cedar glade area, 15 miles southeast of Nashville, April 4, 1949, *Elsie Quarterman 4081* (V).

The most singular characteristic of *L. densipila* is the presence of a dense pilose pubescence on the exterior surface of the siliques. There is no suggestion of the presence of trichomes on the inner face of the valves as in *L. perforata*. The trichomes of the siliques are most frequently simple or forked, but an occasional one can be found with a third branch. This pubescence is not detectable

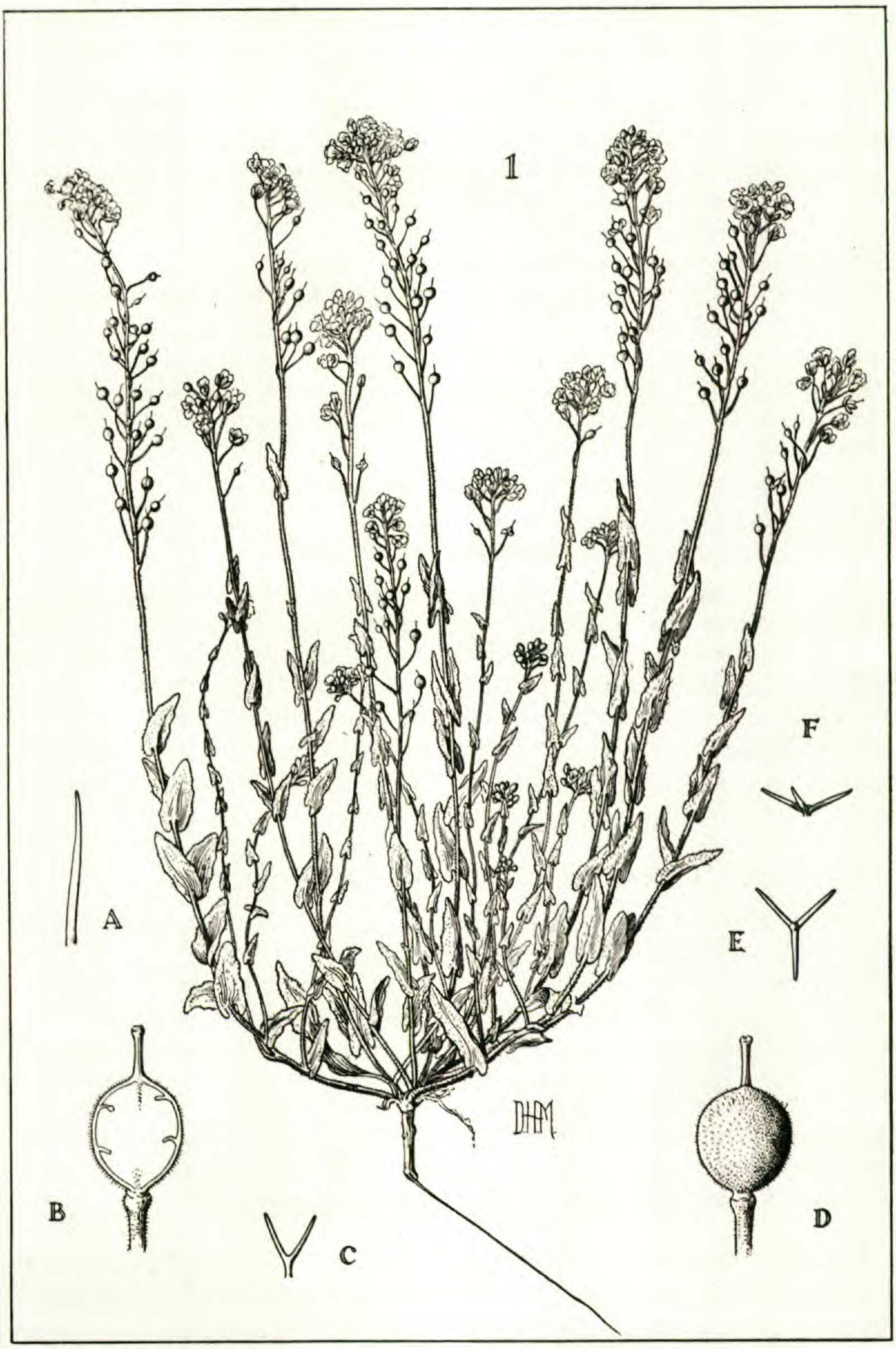

Fig. 1. *Lesquerella densipila*, var. *densipila*. Drawings by Dorothy H. Marsh from Sharp, Felix and Adams no. 11187. Habit × ⅜. A, C, E and F, trichomes × 25. B, replum × 3. D, silique × 3.

with the naked eye in var. *densipila*, and a close inspection with a hand lens is required to see it. Young fruits naturally have a denser covering and the pubescence is more readily seen with low magnification than upon the older siliques. The trichomes are found well up the style, often extending nearly to the middle. This is somewhat unusual in *Lesquerella* for the styles are most often completely glabrous even though the adjacent valves may be densely covered with trichomes. Other features of significance are the auriculate cauline leaves and the stamens with dilated bases. These features are shared by *L. auriculata* and *L. perforata* but they are not general in the genus *Lesquerella*.

Unfortunately the drawing (Fig. 1) does not show the basal leaves, which are definitely petioled. In general outline they vary from lyrately lobed toward runcinate. In most of the twelve specimens in the type series, the basal leaves have been shed.

The two collections from near Duck River do not differ from each other significantly, but specimens taken from the population in Williamson County can be distinguished from the others on trichome size and form. In the latter collection, the trichomes of the siliques average 100μ and are most frequently single. In the Duck River collections the trichomes average 81μ and are most often forked. I could not detect any other correlated differences that seemed significant. The fact that the trichome-size differed in these two populations provided the basis for including in *L. densipila* (as var. *maxima*) a more divergent population with comparatively much longer and larger trichomes and white instead of yellow flowers. This latter population differed so strikingly from *L. densipila* in the field that it was at first thought to represent an undescribed species. However, once it became clear that trichome size was not a reliable distinguishing characteristic, the flower color seemed to represent a less significant difference. However, there is still room for doubt and further field studies may upset the conclusions that now seem valid. The trichomes of the siliques of var. *maxima* differ considerably from plant to plant. In the plants checked, the one with the longest averaged 413μ while that with the shortest showed an average length of 151μ.

3. **Lesquerella perforata** Rollins, sp. nov.

Annual; stems several to many, outer usually decumbent at base, inner erect, simple or branched, 1–2.5 dm. high, densely hirsute below with large spreading mostly simple trichomes, pubescent above with less-spreading mostly branched trichomes; basal leaves lyrately lobed, petiolate, 2–5 cm. long, 5–15 mm. wide, lobes variable, terminal lobe orbicular to ovate, entire or dentate, obtuse to more pointed, lateral lobes broadly oblong, entire or shallowly toothed, becoming remote toward petiole; hirsute on both surfaces, with mostly simple trichomes, marginal trichomes smaller and branched; cauline leaves sessile, auriculate, broadly oblong to nearly ovate, sagittate, dentate, 8–20 mm. long, 4–8 mm. wide, hirsute above with simple trichomes, below with a mixture of simple and branched trichomes; pedicels straight, divaricately ascending, scarcely swollen at apex, 6–12 mm. long, uniformly pubescent with branched trichomes or with a mixture of simple and branched trichomes; sepals oblong, pubescent with a mixture of large and small branched trichomes, 3.5–5 mm. long, 1.5–2 mm. wide; petals white to pale lavender with a yellowish claw, sometimes tinged with light purple when dry, unguiculate, obovate to very broadly spatulate, emarginate to nearly entire, 7–9 mm. long, 5–6 mm. wide; filaments dilated at base, those of paired stamens 4–4.5 mm. long, anthers ca. 1.3–1.5 mm. long; glandular tissue subtending all filaments and nearly surrounding those of the single stamens, with projections between single and paired stamens; siliques inflated, broadly obovoid to subpyriform, very slightly stipitate, sparsely hirsute with large simple or forked trichomes to nearly glabrous on the exterior, densely pubescent with small dendritically branched trichomes on the interior, 4–6 mm. long, widest above the middle, 4–6 mm. wide; septum nearly obsolete, represented by only a narrow band of tissue around the inner margin of the replum; styles 1.5–2.5 mm. long, unexpanded or only very slightly expanded at apex; ovules 4–8 in each silique, funiculi free; immature seeds usually four per silique, flattened, probably with a narrow wing; cotyledons accumbent.

Herba annua; caulibus decumbentibus vel erectis hirsutis 1–2.5 dm. altis; foliis radicalibus petiolatis lyratis hirsutis 2–5 cm. longis, 5–15 mm. latis; foliis caulinis sessilibus auriculatis dentatis hirsutis 8–20 mm. longis, 4–8 mm. latis; pedicellis divaricatis pubescentibus 6–12 mm. longis; sepalis hirsutis; petalis albis obovatis vel late spathulatis 7–9 mm. longis; 5–6 mm. latis; siliquis obovoidis exteriore sparse hirsutis vel glabris, interiore pubescentibus, septis nullis, stylis 1.5–2.5 mm. longis, siliquis 4–8 ovulatis; seminibus immaturis marginatis; cotyledonibus accumbentibus.

Type in the Gray Herbarium, collected in an open field, 5 miles north of Lebanon, Wilson County, Tennessee, March 30, 1952, *Reed C. and Diane Rollins 5207*. Two other collections are known from near Lebanon: April 1, 1934, *A. J. Sharp 83* (UT); March 30, 1952, *Reed C. and Diane Rollins 5208* (G).

The uniqueness of an indument on the interior of the siliques and the absence or near-absence of a septum in this species have

been indicated above. It should be further pointed out that the trichomes on the interior of the siliques are smaller and more highly branched than the few scattered ones on the exterior surface. The latter trichomes tend to resemble some of those of the sepals, pedicels and stems, which are much coarser and less branched. It might be assumed by some that because these characteristics are so different from those of other species of *Lesquerella*, *L. perforata* may not belong to that genus. However, with the exception of the interior pubescence and the virtual lack of a septum, *L. perforata* fits the pattern for *Lesquerella* as a whole very well. It is obviously related to *L. densipila* and *L. auriculata* so that there is every reason to associate it with them.

4. **Lesquerella globosa** (Desv.) S. Wats. Proc. Amer. Acad. **23:** 252. 1888.

Vesicaria globosa Desv. Journ. Bot. **3:** 184. 1814.
Vesicaria Shortii T. & G. Syn. Fl. N. Am. **1:** 102. 1838 (suppl. 668).
Alyssum Shortii Kuntze. Rev. Gen. Pl. **2:** 931. 1891.

Known from localized places in Tennessee, Kentucky, and Ohio. The following Tennessee specimens are representative: Rising Sun Bluff, Cumberland River, on the Devonian Shale, 14 miles below Nashville, April and Sept., 1886, *A. Gattinger s. n.* (G); same locality, May, 1886, *Gattinger s. n.* (UT); Bull Run Fishing Camp, Davidson Co., March 31, 1952, *Reed C. and Diane Rollins 5213* (G); open talus slopes on bluff, Bull Run section, Davidson Co., April 27, 1940, *Jesse M. Shaver 6561* (G, P); King and Queens Bluff, Cumberland River, Montgomery Co., April 27, 1946, *A. & E. Clebach s. n.* (UT).

Preserved in the Gray Herbarium is a fragment, presumably of the type, and a note in the hand of Asa Gray as follows: "Herb. Desv. Vesicaria globulosa Desv.! (no source. Am. Bor. in . . .) = my *V. Shortii*. Probably from Raf. Very small fruits with slender spreading pedicels. Hab. V." Though undated, it is safe to assume that the note was prepared by Gray while consulting the Desveaux Herbarium and that the fragments were obtained at that time. The fragments are unquestionably of the same species as the material cited above. This evidence, plus that adduced independently by Payson (1922) through Dr. Gagnepain, certainly removes all doubt about the proper application of Desveaux's name. It is interesting to note that Gray copied "globulosa," which Gagnepain says is present on the label of the type sheet, instead of "globosa," as published by Desveaux.

The study of a large series of specimens with mature fruits and seeds collected by Jesse M. Shaver permits me to present accurate information upon these structures. In all cases observed there were two funiculi near the apex of the replum in each loculus. These are definitely attached to the septum for one-third to one-half their lengths. Beyond this point a fold of the septum adheres to the funiculus forming a wing of tissue for nearly its entire length. The septum is not tightly stretched across the replum, as in most species of *Lesquerella*, but has the capacity to stretch fully into one loculus or the other if asymmetrical pressure is brought about by seed development in one loculus and not the other. The septum normally forms a partial pouch around the seed or seeds by enfolding them. I have not seen this feature in any other species of *Lesquerella* and it seems reasonable to infer from it that the siliques of this species or at least its progenitors were at one time considerably larger than at present. The large size of the seeds compared to the locule size lends support to this supposition. When but a single seed develops in a silique, it pushes the septum into the opposite loculus and being nearly round, fills the entire space. If one seed develops in each loculus, these take on a hemispherical shape on the outer side conforming to the inner surface of the valve, and a flattened surface toward the septum, presumably due to the compression tension exerted by the two seeds on opposite sides of the septum. The development of one seed in each loculus is most frequent but quite often two seeds mature in one loculus or the other or occasionally in both. When this happens, the seeds are reduced in size and there are two beveled surfaces on the inner side as described by Murley (1951), one toward the septum and one toward the adjacent seed. The cotyledons are normally accumbent, but the radicle may be pushed to one side due to the effects of crowding.

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